MycoKeys 84: 35–55 (2021)
doi: 10.3897/mycokeys.84.71227
https://mycokeys.pensoft.net

RESEARCH ARTICLE

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Two new calcicolous caloplacoid lichens from South Korea, with a taxonomic key to the species of *Huriella* and *Squamulea*

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Academic editor: Gerhard Rambold | Received 7 July 2021 | Accepted 20 September 2021 | Published 01 November 2021

Citation: Lee BG, Hur J-S (2021) Two new calcicolous caloplacoid lichens from South Korea, with a taxonomic key to the species of *Huriella* and *Squamulea*. MycoKeys 84: 35–55. https://doi.org/10.3897/mycokeys.84.71227

Abstract

Pyrenodesmia rugosa Lee & Hur and *Huriella aeruginosa* Lee & Hur are described as new lichen-forming fungi from a calcareous mountain of South Korea. *Pyrenodesmia rugosa* is distinguishable from *Pyrenodesmia micromontana* (Frolov, Wilk & Vondrák) Hafellner & Türk, the most similar species, by thicker thallus, rugose areoles, larger apothecia, shorter hymenium, shorter hypothecium and narrower tip cells of paraphyses. *Huriella aeruginosa*, the second new species, differs from '*Squamulea*' *chelonia* Bungartz & Søchting by dark greenish-grey to grey thallus without pruina, gold to yellow-brown epihymenium, larger ascospores and thallus K– and KC– reaction. Molecular analyses employing internal transcribed spacer (ITS), mitochondrial small subunit (mtSSU) and nuclear large subunit ribosomal RNA (LSU) sequences strongly support the two caloplacoid species to be distinct in their genera. A surrogate key is provided to assist in the identification of all 20 taxa in *Huriella* and *Squamulea*.

Keywords

Biodiversity, phylogeny, saxicolous, taxonomy, Teloschistaceae

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Introduction

Many lichens are only detected in calcareous areas, particularly for crustaceous lichens, as many plants are never found, except on calcareous rocks and soils (Watson 1918; Kossowska 2008; Pykälä et al. 2017). Caloplacoid lichens have been discovered in calcareous areas, such as *Pyrenodesmia albopustulata* (Khodos. & S.Y. Kondr.) I.V. Frolov & Vondrák, *P. badioreagens* (Tretiach & Muggia) Søchting, Arup & Frödén, *P. concreticola* (Vondrák & Khodos.) Søchting, Arup & Frödén, *P. erodens* (Tretiach, Pinna & Grube) Søchting, Arup & Frödén, '*Squamulea*' *chelonia*, *Squamulea galactophylla* (Tuck.) Arup, Søchting & Frödén, '*Squamulea*' *humboldtiana* Bungartz & Søchting, *Squamulea parviloba* (Wetmore) Arup, Søchting & Frödén and *S. subsoluta* (Nyl.) Arup, Søchting & Frödén (Khodosovtsev et al. 2002; Tretiach et al. 2003; Wetmore 2003; Tretiach and Muggia 2006; Vondrák 2008; Arup 2013; Bungartz et al. 2020). Many lichens have been introduced from the calcareous areas in Korea, such as *Anema decipiens* (A. Massal.) Forssell, *Astroplaca loekoesiana* S.Y. Kondr., Farkas, J.J. Woo & Hur, *Caeruleum heppii* (Nägeli ex Körb.) K. Knudsen & Arcadia, *Clauzadea metzleri* (Körb.) Clauzade & Cl. Roux, *Clauzadea monticola* (Ach.) Hafellner & Bellem., *Collema auriforme* (With.) Coppins & J.R. Laundon, *C. cristatum* (L.) Weber ex F.H. Wigg., *Endocarpon pallidum* Ach., *Halecania pakistanica* van den Boom & Elix, *Heppia adglutinata* A. Massal., *Ionaspis epulotica* (Ach.) Blomb. & Forssell, *Lecania turicensis* (Hepp) Müll. Arg., *Lecanora albescens* (Hoffm.) Branth & Rostr., *L. semipallida* H. Magn., *Lemmopsis arnoldiana* (Hepp) Zahlbr., *Lichinella cribellifera* (Nyl.) P.P. Moreno & Egea, *L. stipatula* Nyl., *Placynthium tantaleum* (Hepp) Hue, *Porina fluminea* P.M. McCarthy & P.N. Johnson, *Psorotichia frustulosa* Anzi, *P. schaereri* (A. Massal.) Arnold, *Pterygiopsis affinis* (A. Massal.) Henssen, *Pyrenocarpon* aff. *thelostomum* (Ach. ex J. Harriman) Coppins & Aptroot, *Rufoplaca aesanensis* S.Y. Kondr. & Hur, *Staurothele frustulenta* Vain., *Synalissa ramulosa* (Hoffm.) Körb., *Thyrea confusa* Henssen, *Toninia poeltiana* S.Y. Kondr., Lőkös & Hur, *T. tristis* (Th. Fr.) Th. Fr. and *Verrucaria muralis* Ach. (van den Boom and Elix 2005; Joshi et al. 2009; Schultz and Moon 2011; Aptroot and Moon 2014, 2015, Kondratyuk et al. 2016a, 2016b, 2017a, 2020). Although calcicolous caloplacoid lichens were little reported from Korea in the past, for example, *Rufoplaca aesanensis*, it is assumed that diverse caloplacoid lichens inhabit calcareous rocks and soils which were previously reported from just rock or soil without specifying specific rock or soil types.

This study describes two new calcicolous caloplacoid lichens in the genera *Pyrenodesmia* and *Huriella*. Qualified field surveys for the lichen diversity on the Baekdudaegan Mountains, the main mountain range stretching across the entire Korean Peninsula, were accomplished during the summer of 2020 and a few dozen specimens of caloplacoid lichens were collected in Mt. Seokbyung, a calcareous mountain (Fig. 1). We describe them as two new species, *Pyrenodesmia rugosa* and *Huriella aeruginosa*. The specimens are deposited in the herbarium of the Baekdudaegan National Arboretum (KBA), South Korea.

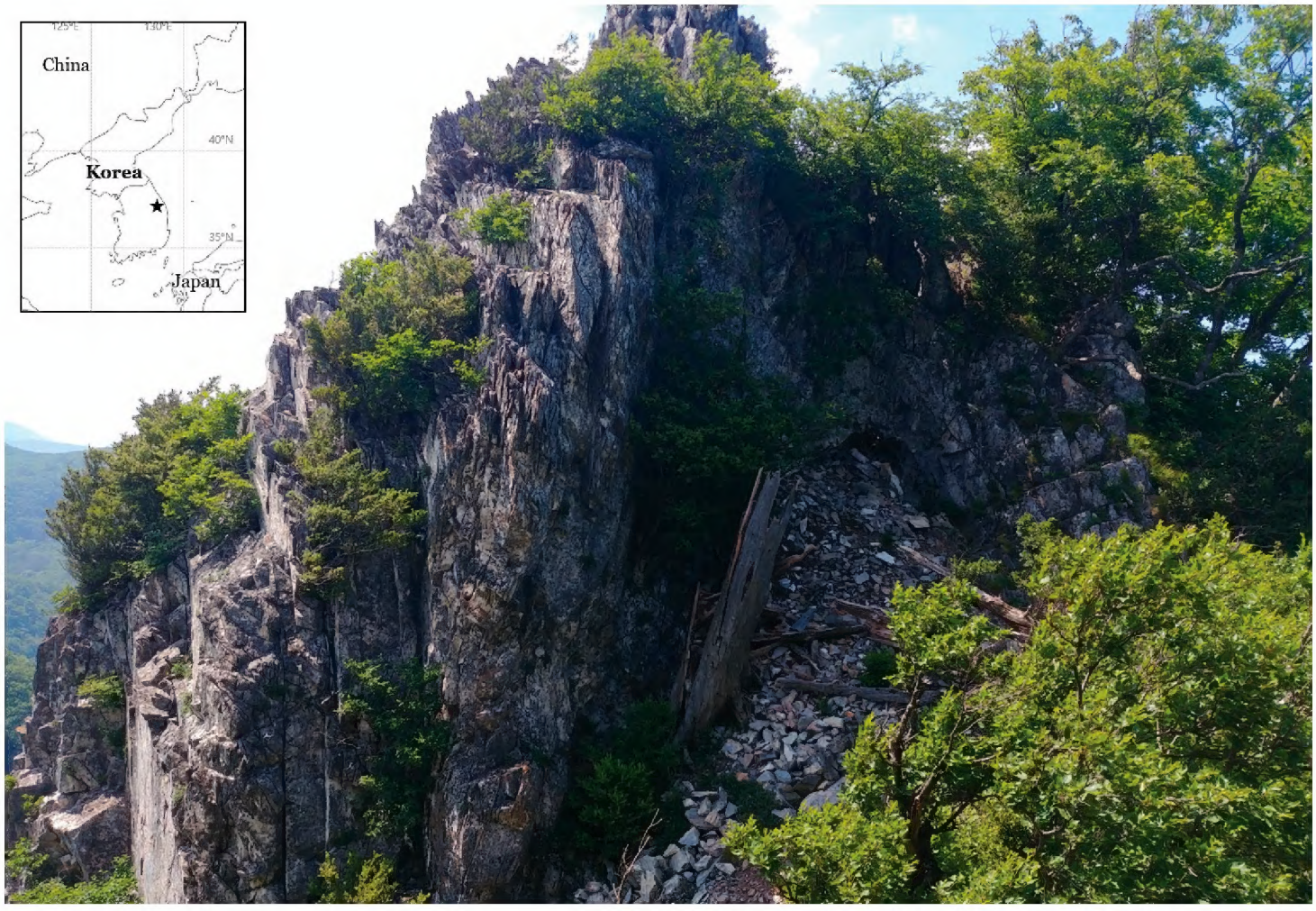

Figure 1. Specific collection site for two new species, representing the habitat/landscape and the location (black star mark).

Materials and methods

Morphological and chemical analyses

Hand-cut sections were prepared with a razor blade under a stereomicroscope (Olympus optical SZ51; Olympus, Tokyo, Japan), examined under a compound microscope (Nikon Eclipse E400; Nikon, Tokyo, Japan) and imaged using a software programme (NIS-Elements D; Nikon, Tokyo, Japan) and a DS-Fi3 camera (Nikon, Tokyo, Japan), mounted on a Nikon Eclipse Ni-U microscope (Nikon, Tokyo, Japan). The ascospores were investigated at 1000× magnification in water. The length and width of the ascospores were measured and the range of spore sizes was shown with average, standard deviation and number of measured spores. Thin-layer chromatography (TLC) was performed using solvent systems A and C according to standard methods (Orange et al. 2001).

Isolation, DNA extraction, amplification and sequencing

Hand-cut sections of ascomata or thallus from all collected specimens were prepared for DNA isolation and DNA was extracted with a NucleoSpin Plant II Kit in line with the manufacturer's instructions (Macherey-Nagel, Düren, Germany). PCR amplification for the internal transcribed spacer region (ITS1-5.8S-ITS2 rDNA), the mitochondrial

small subunit and the nuclear large subunit ribosomal RNA genes was achieved using Bioneer's AccuPower PCR Premix (Bioneer, Daejeon, Korea) in 20-µl tubes and primers ITS5 and ITS4 (White et al. 1990), mrSSU1 and mrSSU3R (Zoller et al. 1999) and LR0R and LR5 (Rehner and Samuels 1994), respectively. The PCR thermal cycling parameters used were 95 °C (15 sec), followed by 35 cycles of 95 °C (45 sec), 54 °C (45 sec) and 72 °C (1 min) and a final extension at 72 °C (7 min), based on Ekman (2001). DNA sequences were generated by the genomic research company Macrogen (Seoul, Korea).

Phylogenetic analyses

All ITS, mtSSU and LSU sequences were aligned and edited manually using ClustalW in Bioedit V.7.2.6.1 (Hall 1999). All missing and ambiguously aligned data and parsimony-uninformative positions were removed and only parsimony-informative regions were finally analysed in MEGA X (Stecher et al. 2020). The final alignment comprised 878 (ITS), 900 (mtSSU) and 1701 (LSU) columns for *Pyrenodesmia*. In them, variable regions were 178 (ITS), 42 (mtSSU) and 618 (LSU). The phylogenetically-informative regions were 356 (ITS), 55 (mtSSU) and 98 (LSU). The final alignment for *Huriella* and *Squamulea* comprised 693 (ITS) columns. In them, variable regions were 78 (ITS). Finally, the phylogenetically-informative region was 246 (ITS). Phylogenetic trees with bootstrap values were obtained in RAxML GUI 2.0 beta (Edler et al. 2019) using the Maximum Likelihood method with a rapid bootstrap with 1000 bootstrap replications and GTR GAMMA for the substitution matrix. The posterior probabilities were obtained in BEAST 2.6.4 (Bouckaert et al. 2019) using the HKY (Hasegawa, Kishino and Yano) model, as the appropriate model for nucleotide substitution, based on the Bayesian Information Criterion (BIC) (Schwarz 1978) as evaluated by bModelTest (Bouckaert and Drummond 2017), empirical base frequencies, gamma for the site heterogeneity model, four categories for gamma and a 10,000,000 Markov Chain Monte Carlo chain length with a 10,000-echo state screening and 1000 log parameters. Then, a consensus tree was constructed in TreeAnnotator 2.6.4 (Bouckaert et al. 2019) with a burn-in of 5000, no posterior probability limit, a maximum clade credibility tree for the target tree type and median node heights. All trees were displayed in FigTree 1.4.2 (Rambaut 2014) and edited in Microsoft Paint. The bootstrapping and Bayesian analyses were repeated three times for the result consistency and no significant differences were shown for the tree shapes and branch values. The phylogenetic trees and DNA sequence alignments are deposited in TreeBASE under the study ID 28190.

Results and discussion

Phylogenetic analyses

Three independent phylogenetic trees for *Pyrenodesmia* and one independent phylogenetic tree for *Squamulea* were produced from 165 sequences (96 for ITS, 37 for mtSSU and 32 for LSU) from GenBank and four new sequences (two for ITS, one for mtSSU

and one for LSU) for the new species (Table 1). *Pyrenodesmia rugosa*, a new species, was positioned in the genus *Pyrenodesmia* in all ITS, mtSSU and LSU trees. The ITS tree described that the new species was solely located without any clade. Several species closely positioned with the new species were *Pyrenodesmia aractina* (Fr.) S.Y. Kondr., *P. bicolor* (H. Magn.) S.Y. Kondr. and *P. haematites* (Chaub. ex St.-Amans) S.Y. Kondr., represented by a bootstrap value of 84 and a posterior probability of 0.73 (not shown) for the branch (Fig. 2). The mtSSU tree showed that the new species was located in a clade with *Pyrenodesmia albopruinosa* (Arnold) S.Y. Kondr. and *P. micromontana*, represented by a bootstrap value of 72 and a posterior probability of 1.0 for the branch (Fig. 3). The LSU tree depicted that the new species was positioned solely without any clade. Several species, such as *Kuettlingeria cretensis* (Zahlbr.) I.V. Frolov & Vondrák, *K. neotaurica* (Vondrák, Khodos., Arup & Søchting) I.V. Frolov, Vondrák & Arup, *Pyrenodesmia albopustulata*, *P. chalybaea* (Fr.) A. Massal., *P. helygeoides* (Vain.) Arnold, *P. microstepposa* (Frolov, Nadyeina, Khodos. & Vondrák) Hafellner & Türk, *P. molariformis* (Frolov, Vondrák, Nadyeina & Khodos.) S.Y. Kondr., *P. pratensis* (Wetmore) Frolov & Vondrák and *P. variabilis* (Pers.) A. Massal. are situated close to the new species (Fig. 4). *Huriella aeruginosa*, the second new species, was located in *Huriella* in the ITS tree. The ITS tree described that the new species was positioned in a clade with '*Squamulea*' *subsoluta* and '*Squamulea*' sp., represented by a bootstrap value of 35 (not shown) without a posterior probability as the Maximum Likelihood analysis did not match with the Bayesian Inference for the clade (Fig. 5). Although the two closely located sequences were named for *Squamulea* in the beginning, they are close to *Huriella*, not *Squamulea*. The two sequences are arranged in the genus *Huriella* with the new species. The phylogenetic analyses did not designate any species identical to the two new species in each genus *Pyrenodesmia* and *Huriella*.

Taxonomy

Pyrenodesmia rugosa **B.G. Lee & J.-S. Hur, sp. nov.**
MycoBank No: 839184
Fig. 6

Diagnosis. *Pyrenodesmia rugosa* differs from *P. micromontana* by thicker thallus (125–200 µm vs. 95–125 µm), rugose areoles (vs. flat areoles), larger apothecia (0.2–0.7 mm diam. vs. 0.2–0.4 mm diam.), shorter hymenium (60–70 µm vs. 80–100 µm), shorter hypothecium (50–55 µm vs. 80–100 µm) and narrower tip cells of paraphyses (3–4.5 µm vs. 5–6 µm).

Type. South Korea, Gangwon Province, Gangneung, Okgye-myeon, Mt. Seokbyung (summit), 37°35.21'N, 128°53.87'E, 1,072 m alt., on calcareous rock, 17 June 2020, B.G.Lee & H.J.Lee 2020-000902, with *Athallia* cf. *vitellinula* (Nyl.) Arup, Frödén & Søchting, *Bagliettoa baldensis* (A. Massal.) Vězda, *Catillaria lenticularis* (Ach.) Th. Fr. and *Staurothele* aff. *succedens* (Rehm) Arnold (holotype: BDNA-L-0001102!); same locality, on calcareous rock, 17 June 2020, B.G.Lee & H.J.Lee 2020-000899, with *Athallia* cf. *holocarpa* (Hoffm.) Arup, Frödén & Søchting and *Staurothele* cf. *rupifraga*

Table 1. Species list and DNA sequence information employed for phylogenetic analysis.

No	Species	ID (ITS)	ID (mtSSU)	ID (LSU)	Voucher
1	*Amundsenia approximata*	KJ789965			L08179 (LD)
2	*Amundsenia austrocontinentalis*	KJ789962			21966 (HO)
3	*Athallia holocarpa*	MG954144			Vondrak 18072
4	*Athallia vitellinula*	FJ346556			Arup L03052
5	*Caloplaca monacensis*	MG773668	MG773679		Malicek 8255
6	*Caloplaca* sp.	KC611244			CBFS:JV6943
7	*Erichansenia sauronii*	KC179120			Sochting 7654
8	***Huriella aeruginosa***	**MW832829**			**BDNA-L-0001072**
9	*Huriella flakusii*	MT967442			Bungartz 4131 (CDS 28162)
10	*Huriella flakusii*	MT967443			Bungartz 4157 (CDS 28188)
11	*Huriella flakusii*	MT967444			Aptroot 65261 (CDS 31847)
12	*Huriella loekoesiana*	KY614406			KoLRI 15423
13	*Huriella loekoesiana*	KY614407			KoLRI 19017
14	*Huriella loekoesiana*	KY614408			KoLRI 40141
15	*Huriella loekoesiana*	KY614409			KoLRI 40236
16	*Huriella loekoesiana*	KY614410			KoLRI 40238
17	*Huriella loekoesiana*	MK499351			HKAS 102112
18	*Huriella* sp.	MN108089			KRAM-L-70242
19	*Kuettlingeria albolutescens*	KC179423	KC179502	MT952898	Arup L09030 (LD)
20	*Kuettlingeria areolata*	MN305805	MN305825	MN305847	Vondrak 10843
21	*Kuettlingeria atroflava*	MH104921	MH100775		Vondrak 8723 (PRA)
22	*Kuettlingeria cretensis*	MH104925	MH100783	MH100751	Frolov s.n.
23	*Kuettlingeria diphyodes*	MH104926	MH100785	MH100753	Frolov 1430
24	*Kuettlingeria emilii*	KC416102	MH100787	MH100754	JV9358
25	*Kuettlingeria erythrocarpa*	KC179427	KC179506	KC179173	Arup L07109 (LD)
26	*Kuettlingeria neotaurica*	MN305807	MN305829	MN305849	Vondrak 7213
27	*Kuettlingeria percrocata*	MH104931	MH100794		Vondrak 4634 (PRA)
28	*Kuettlingeria soralifera*	MN305808	MN305830	MN305850	Vondrak 10813
29	*Kuettlingeria aff. soralifera*	JN641781			CBFS:JV8325
30	*Kuettlingeria teicholyta*	MH104935	MH100797	MH100767	Vondrak 6943 (PRA)
31	*Kuettlingeria xerica*	MN305809	MN305831	MN305851	Vondrak 14544
32	*Kuettlingeria aff. xerica*	HQ611275			CBFS:JV7618
33	*Lendemeriella borealis*	MG954129			Vondrak 11073
34	*Lendemeriella exsecuta*	MG954227			Spribille 24441
35	*Lendemeriella nivalis*	MG954222			Spribille 29306
36	*Lendemeriella reptans*	MH104934	MH100796	MH100766	Lendemer 48186 (NY)
37	*Lendemeriella sorocarpa*	MG954132			Vondrak12695
38	*Lendemeriella tornoensis*	MG954221			Spribille 29473
39	*Olegblumia demissa*	KT220203	KT220221	KT220212	SK C65
40	*Pyrenodesmia aetnensis*	EU639590	KT291476		X. Llimona (BCN)
41	*Pyrenodesmia albopruinosa*	EF093577	MH100770		TSB 37658
42	*Pyrenodesmia albopustulata*	MH104918	MH100771	MH100741	Vondrak 10463 (PRA)
43	*Pyrenodesmia alociza*	EF090931	MH100772	MH100742	TSB 37735
44	*Pyrenodesmia aractina*	GU723415			Bornholm 5907
45	*Pyrenodesmia aractina*	GU723418			Bornholm 6911
46	*Pyrenodesmia aractina*	MH104919	MH100773		Vondrak 6702 (PRA)
47	*Pyrenodesmia atroalba*	MH104920	MH100774		Spribille s.n.
48	*Pyrenodesmia badioreagens*	EF081035	MH100776	MH100745	TSB 36422
49	*Pyrenodesmia bicolor*	MH104922	MH100777	MH100746	Vondrak 10373 (PRA)

No	Species	ID (ITS)	ID (mtSSU)	ID (LSU)	Voucher
50	*Pyrenodesmia ceracea*	HQ234603			BM-6656
51	*Pyrenodesmia chalybaea*	KC884498	MH100779	MH100747	CBFS:JV4059
52	*Pyrenodesmia circumalbata*	MH104923	MH100780	MH100748	Halici s.n.
53	*Pyrenodesmia concreticola*	KC884506	MH100781	MH100749	CBFS:JV9443
54	*Pyrenodesmia duplicata*	HQ611272			TUR-V-7513
55	*Pyrenodesmia erodens*	MH104927	MH100788	MH100755	Vondrak 12733 (PRA)
56	*Pyrenodesmia haematites*	GU723420	MH100789	MH100756	Vondrak 7278 (PRA)
57	*Pyrenodesmia haematites*	GU723421			JS280
58	*Pyrenodesmia haematites*	MH104928			Vondrak 7278 (PRA)
59	*Pyrenodesmia helygeoides*	MH104929	MH100790	MH100757	Frolov 1414
60	*Pyrenodesmia micromarina*	NR_156257			CBFS:JV8199
61	*Pyrenodesmia micromarina*		MH100791	MH100758	Vondrak 7236 (PRA)
62	*Pyrenodesmia micromontana*	NR_158297	MH100792	MH100759	CBFS:JV9467
63	*Pyrenodesmia microstepposa*	NR_156260		MH100760	CBFS:JV9141
64	*Pyrenodesmia molariformis*	KC416145	MH100793	MH100761	Nadyeina 132 (KW)
65	*Pyrenodesmia obscurella*	MH104938		MH100762	Vondrak 7641 (PRA)
66	*Pyrenodesmia peliophylla*	MG733135			Jason Hollinger:16476
67	*Pyrenodesmia pratensis*	MH104933	MH100795	MH100765	MIN 891605
68	***Pyrenodesmia rugosa***	**MW832828**	**MW832825**	**MW832904**	**BDNA-L-0001099**
69	*Pyrenodesmia transcaspica*	MH104936	MH100799	MH100768	Vondrak 9430 (PRA)
70	*Pyrenodesmia variabilis*	KT291466	KT291514	KT291561	Ulf Arup L07196 (LD)
71	*Shackletonia buelliae*	KC179117			Sochting 7583
72	*Shackletonia siphonospora*	KC179121			Sochting 7883
73	*Squamulea galactophylla*	KC179122			Morse 10997 (LD)
74	*Squamulea kiamae*	KC179123			Kondratyuk 20480 (LD)
75	*Squamulea parviloba*	KC179124			Wetmore 87830 (LD)
76	*Squamulea squamosa*	MT967462			Moberg 8782 (UPS)
77	*Squamulea squamosa*	KC179125			Karnefelt AM960105 (LD)
78	*Squamulea 'squamosa'*	MT967465			Bungartz 7428 (CDS 37915)
79	*Squamulea subsoluta*	AF353954			Arup L97072
80	*Squamulea subsoluta*	DQ173238			Arup L97829
81	*Squamulea subsoluta*	KJ133480			KoLRI 011067
82	'*Squamulea' chelonia*	MT967448			Bungartz 4521 (CDS 28607)
83	'*Squamulea' chelonia*	MT967451			Bungartz 9251 (CDS 46069)
84	'*Squamulea' chelonia*	MT967452			Bungartz 6146 (CDS 34358)
85	'*Squamulea' humboldtiana*	MT967439			Buck 29560 (MIN)
86	'*Squamulea' humboldtiana*	MT967440			Bungartz 4711B (CDS 56235)
87	'*Squamulea' humboldtiana*	MT967441			Bungartz 9985 (CDS 47354)
88	'*Squamulea' oceanica*	MT967445			Yánez-Ayabaca 2023 (CDS 48373)
89	'*Squamulea' oceanica*	MT967446			Bungartz 10152 (CDS 47571)
90	'*Squamulea' oceanica*	MT967447			Bungartz 9857 (CDS 47195)
91	'*Squamulea' osseophila*	MT967455			Aptroot 65489 (CDS 32078)
92	'*Squamulea' phyllidizans*	MT967456			Aptroot 65468 (CDS 32057)

No	Species	ID (ITS)	ID (mtSSU)	ID (LSU)	Voucher
93	'*Squamulea*' *phyllidizans*	MT967457			Bungartz 4710 (CDS 28808)
94	'*Squamulea*' *phyllidizans*	MT967458			Bungartz 4158 (CDS 28189)
95	'*Squamulea*' *subsoluta*	KJ133481			KoLRI 012491
96	'*Squamulea*' sp.	MG954160			Vondrak 18682
97	*Usnochroma carphineum*	KC179468	KC179598	KC179259	Roux s.n.
98	*Usnochroma scoriophilum*	JQ301664	JQ301496	JQ301560	P. & B. v.d. Boom 38386
	Overall	**98**	**38**	**33**	

DNA sequences which were generated in this study, i.e. two new species, such as *Pyrenodesmia rugosa* and *Huriella aeruginosa* are presented in bold. All others were obtained from GenBank. The species names are followed by GenBank accession numbers and voucher information. ITS, internal transcribed spacer; mtSSU, mitochondrial small subunit; LSU, large subunit; Voucher, voucher information.

(A. Massal.) Arnold (paratype: BDNA-L-0001099; GenBank MW832828 for ITS, MW832825 for mtSSU and MW832804 for LSU).

Thallus saxicolous (calcicolous), crustose, mainly areolate or slightly rimose, rugose, greyish-brown to pale brown, often with orange spots, margin indeterminate or determinate when placodioid areoles are arranged around edge, vegetative propagules absent, areoles 0.4–1.0 mm diam., 125–200 µm thick; cortex hyaline with pale brown pigment layer, pale brown pigment K+ purple, 10–40 µm thick, cortical cells granular, 5–10 µm diam., with epinecral layer, 5–7 µm thick; medulla 60–110 µm thick below algal layer or inconspicuous and algal layer shown just above substrate; photobiont coccoid, cells globose to oval, 5–15 µm diam., algal layer 50–70 µm thick. Small crystals present between algal cells, not dissolving in K. Prothallus absent.

Apothecia abundant, scattered or concentrated in centre, rounded, often contiguous or even coalescent when mature, emerging on the surface of thallus, immersed or adnate, slightly constricted at the base, 0.2–0.7 mm diam. Disc flat when young and flat or concave when mature, often white pruinose, black, 200–300 µm thick; zeorine, margin persistent, slightly prominent, generally entire or rarely slightly crenulate, thalline margin paler to disc and showing brown colour, often inconspicuous due to locating below proper margin, proper margin concolorous to disc. Amphithecium present, with small crystals between algal cells, not dissolving in K, 80–130 µm wide laterally, algal layers continuous to the base and underlying the hypothecium, algal cells 5–15 µm diam., cortical layer hyaline with pale brownish pigment at periphery, 10–40 µm thick. Parathecium well-developed, hyaline, but grey with slightly brown pigment concolorous to epihymenium at periphery, 20–40 µm wide laterally and 50–90 µm wide at periphery. Epihymenium grey with slightly brown pigment, K+ purple, tiny granules abundant on surface, not dissolving in K, 5–10 µm high. Hymenium hyaline, 60–70 µm high. Hypothecium hyaline, base open and extending downwards, 50–55 µm high. Oil droplets present in upper hypothecium, but absent in hymenium. Paraphyses septate, often anastomosing, 2–2.5 µm wide, generally simple, but occasionally branched at tips, tips slightly swollen, not pigmented, 3.0–4.5 µm wide. Asci oblong to narrowly clavate, 8-spored, 52–60 × 14–18 µm (n = 5). Ascospores ellipsoid, 1-septate, polarilocular when mature or narrow septum remaining, hyaline

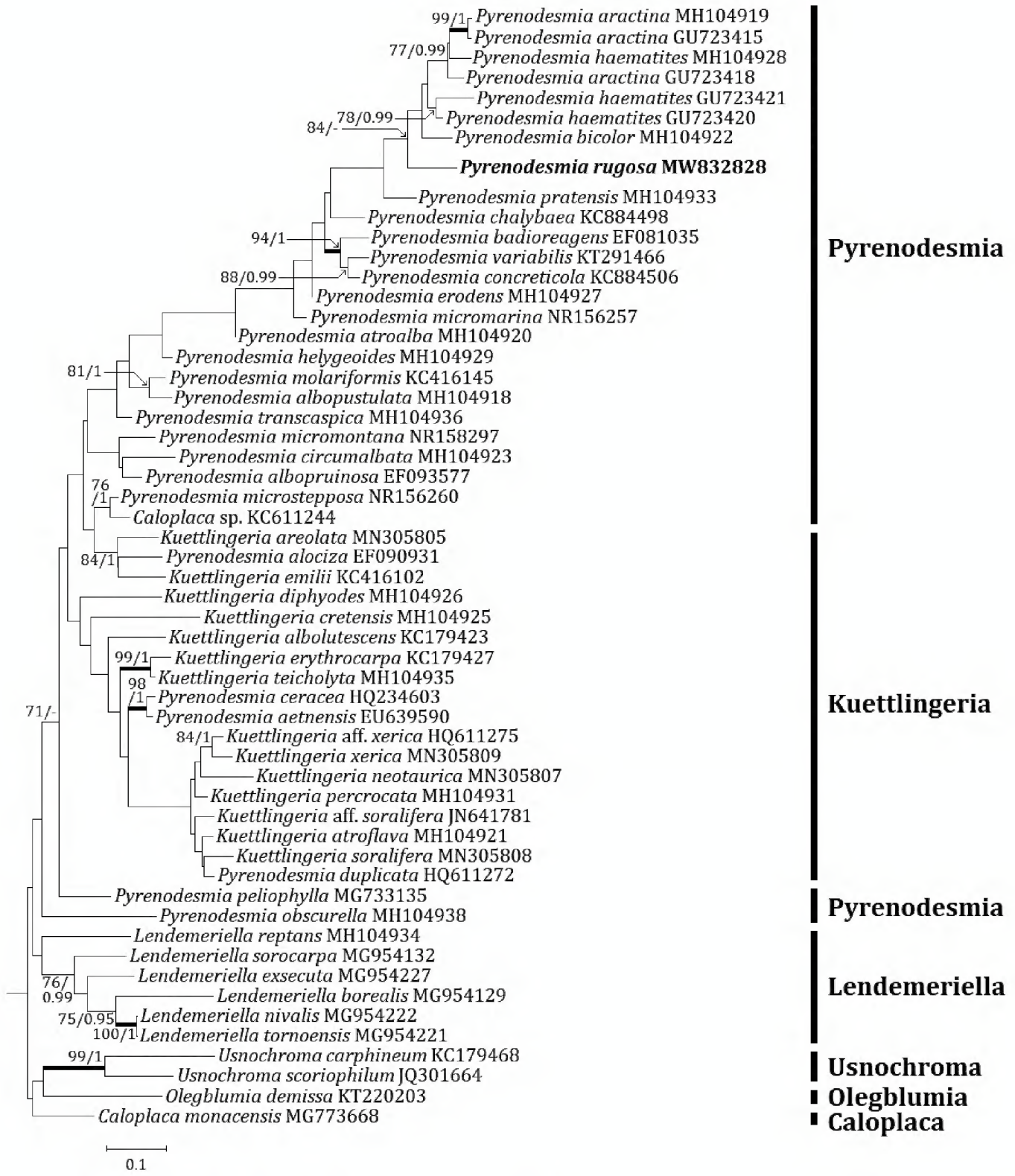

Figure 2. Phylogenetic relationships amongst available species in the genus *Pyrenodesmia*, based on a Maximum Likelihood analysis of the dataset of ITS sequences. The tree was rooted with the sequences of the genera *Caloplaca*, *Lendemeriella*, *Olegblumia* and *Usnochroma*. Maximum Likelihood bootstrap values ≥ 70% and posterior probabilities ≥ 95% are shown above internal branches. Branches with bootstrap values ≥ 90% are shown in bold. The new species *Pyrenodesmia rugosa* is presented in bold and all species names are followed by the GenBank accession numbers. Reference Table 1 provides the species related to the specific GenBank accession numbers and voucher information.

permanently, 11–18 × 5.5–11 µm (mean = 14.1 × 7.6 µm; SD = 1.6(L), 1.0(W); L/W ratio 1.5–2.5, ratio mean = 1.9, ratio SD = 0.3; n = 105), septum 1.5–3.0 µm. Pycnidia not detected.

Chemistry. Thallus K–, KC–, C–, Pd–. Epihymenium K+ purple. Hymenium I+ blue. UV–. No lichen substance was detected by TLC.

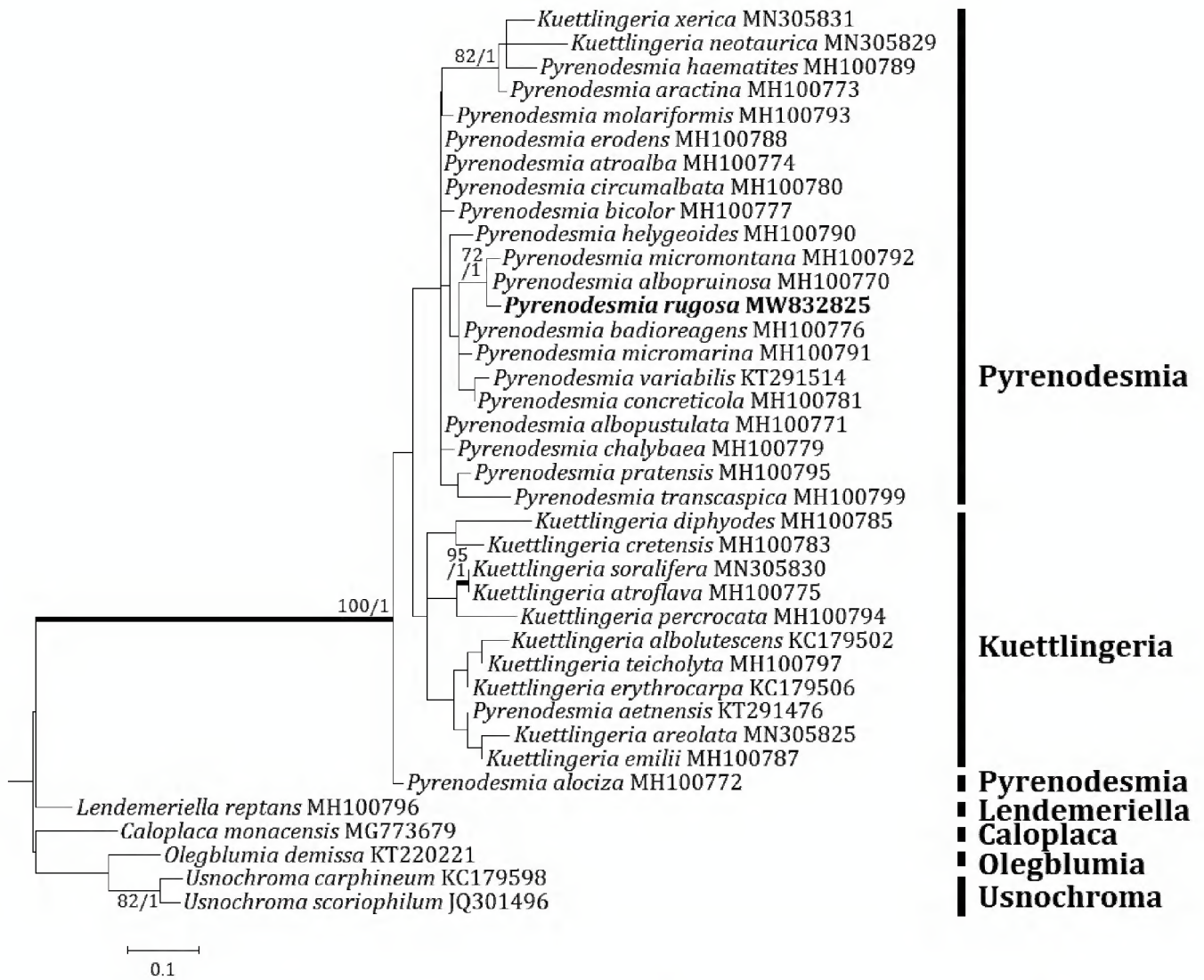

Figure 3. Phylogenetic relationships amongst available species in the genus *Pyrenodesmia*, based on a Maximum Likelihood analysis of the dataset of the mitochondrial small subunit (mtSSU) sequences. The tree was rooted with five sequences of the genera *Caloplaca*, *Lendemeriella*, *Olegblumia* and *Usnochroma*. Maximum Likelihood bootstrap values ≥ 70% and posterior probabilities ≥ 95% are shown above internal branches. Branches with bootstrap values ≥ 90% are shown in bold. The new species *Pyrenodesmia rugosa* is presented in bold and all species names are followed by the GenBank accession numbers. Reference Table 1 provides the species related to the specific GenBank accession numbers and voucher information.

Distribution and ecology. The species occurs on the calcareous rock. The species is currently known from the type collections.

Etymology. The species epithet indicates the lichen's thallus texture, rugose or wrinkled, which is the key characteristic distinguished from closely-related calcicolous species in the genus *Pyrenodesmia*.

Notes. The new speices is similar to *P. micromontana*, *P. microstepposa* and *Caloplaca micromarina* Frolov, Khodos. & Vondrák in having epilithic thallus without vegetative propagules, small apothecia generally less than 0.5 mm diameter and the substrate preference to calcareous rocks. The new species differs from *P. micromontana* by thicker thallus (125–200 μm vs. 95–125 μm), rugose areoles (vs. flat areoles), larger apothecia (0.2–0.7 mm diam. vs. 0.2–0.4 mm diam.), shorter hymenium (60–70 μm vs. 80–100 μm), shorter hypothecium (50–55 μm vs. 80–100 μm) and narrower tip cells of paraphyses (3–4.5 μm vs. 5–6 μm) (Frolov et al. 2016).

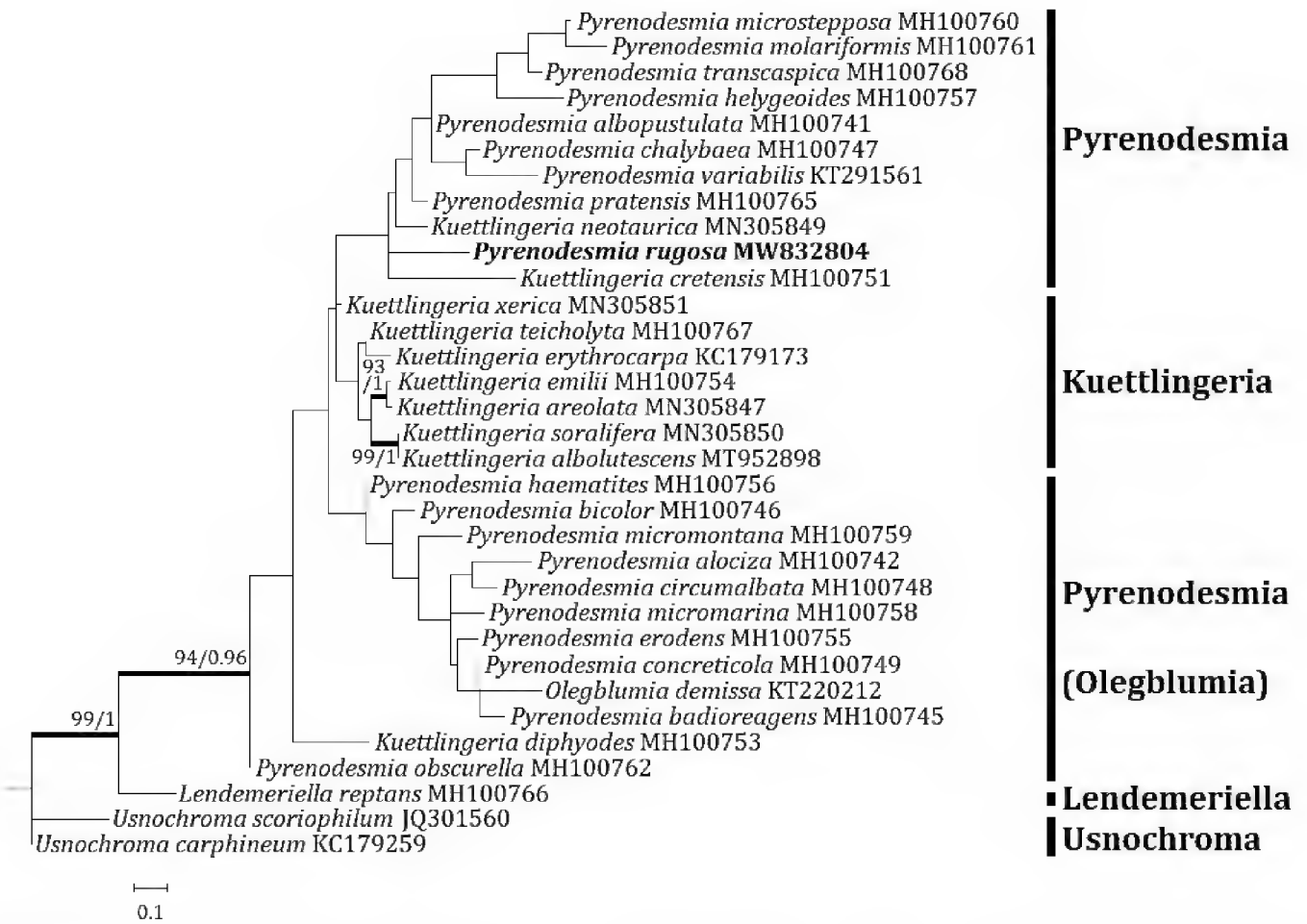

Figure 4. Phylogenetic relationships amongst available species in the genus *Pyrenodesmia* , based on a Maximum Likelihood analysis of the dataset of the nuclear large subunit ribosomal RNA (LSU) sequences. The tree was rooted with three sequences of the genera *Lendemeriella* and *Usnochroma*. Maximum Likelihood bootstrap values ≥ 70% and posterior probabilities ≥ 95% are shown above internal branches. Branches with bootstrap values ≥ 90% are shown in bold. The new species *Pyrenodesmia rugosa* is presented in bold and all species names are followed by the GenBank accession numbers. Reference Table 1 provides the species related to the specific GenBank accession numbers and voucher information.

The new species is different from *P. microstepposa* by darker thallus (greyish-brown to pale brown vs. ochre, grey or grey-white), rugose thallus (vs. flat thallus), thinner thallus (125–200 μm vs. 85–370 μm), smaller algal cells (5–15 μm diam. vs. 13.5–20.5 μm diam.), presence of pruina on disc (vs. absence of it), absence of oil droplets in hymenium (vs. presence of it), greyish epihymenium (vs. brownish epihymenium), wider ascospores (11–18 × 5.5–11 μm with the L/W ratio of 1.5–2.5 vs. 13.6–18.4 × 6–7.9 μm with the ratio of 1.9–2.9) (Frolov et al. 2016).

The new species is distinguished from *C. micromarina* by darker thallus (greyish-brown to pale brown vs. ochre to grey), rugose thallus (vs. flat thallus), absence of pruina on thallus (vs. presence of it), shorter hymenium (60–70 μm vs. 90–100 μm), shorter septum (1.5–3 μm vs. 2.6–3.4 μm) and the habitat preference to mountain rocks (vs. coastal rocks) (Frolov et al. 2016).

Additional specimens examined: South Korea, Gangwon Province, Okgye-myeon, Mt. Seokbyung (summit), 37°35.21'N, 128°53.87'E, 1,072 m alt., on calcareous rock, 17 June 2020, B.G.Lee & H.J.Lee 2020-000889, with *Bagliettoa baldensis*, *Catillaria lenticularis*, *Fulgogasparrea decipioides* (Arup) S.Y. Kondr., M.H. Jeong,

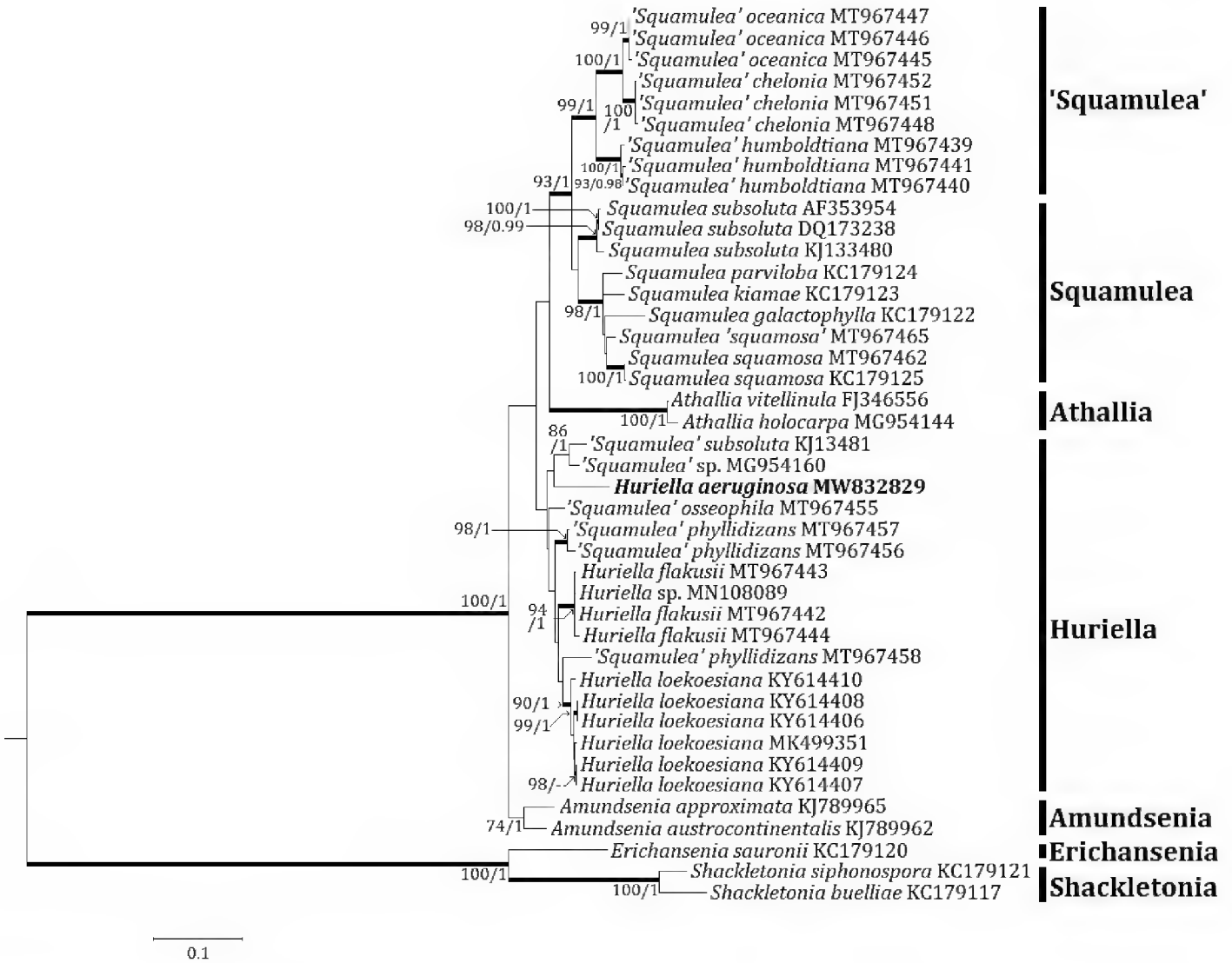

Figure 5. Phylogenetic relationships amongst available species in the genera *Huriella* and *Squamulea*, based on a Maximum Likelihood analysis of the dataset of ITS sequences. The tree was rooted with the sequences of the genera *Amundsenia*, *Erichansenia* and *Shackletonia*. Maximum Likelihood bootstrap values ≥ 70% and posterior probabilities ≥ 95% are shown above internal branches. Branches with bootstrap values ≥ 90% are shown in bold. The new species *Huriella aeruginosa* is presented in bold and all species names are followed by the GenBank accession numbers. Reference Table 1 provides the species related to the specific GenBank accession numbers and voucher information.

Kärnefelt, Elix, A. Thell & Hur and *Laundonia flavovirescens* (Wulfen) S.Y. Kondr., Lőkös & Hur (BDNA-L-0001089); same locality, on calcareous rock, 17 June 2020, B.G.Lee & H.J.Lee 2020-000909, with *Bagliettoa baldensis*, *Rusavskia elegans* (Link) S.Y. Kondr. & Kärnefelt and *Verrucaria nigrescens* Pers. (BDNA-L-0001109); same locality, on calcareous rock, 17 June 2020, B.G.Lee & H.J.Lee 2020-000910, with *Bagliettoa baldensis*, *Catillaria lenticularis* and *Laundonia flavovirescens* (BDNA-L-0001110); same locality, on calcareous rock, 17 June 2020, B.G.Lee & H.J.Lee 2020-000911, with *Athallia* cf. *vitellinula*, *Bagliettoa baldensis*, *Lichenella* sp. and *Rusavskia elegans* (BDNA-L-0001111); same locality, on calcareous rock, 17 June 2020, B.G.Lee & H.J.Lee 2020-000913, with *Athallia* cf. *vitellinula*, *Bagliettoa baldensis*, *Endocarpon* sp., *Laundonia flavovirescens*, *Lichenella* sp. and *Rusavskia elegans* (BDNA-L-0001113); same locality, on calcareous rock, 17 June 2020, B.G.Lee & H.J.Lee 2020-000916, with *Caloplaca* sp., *Endocarpon* sp., *Lichenella* sp. and *Rusavskia elegans* (BDNA-L-0001116).

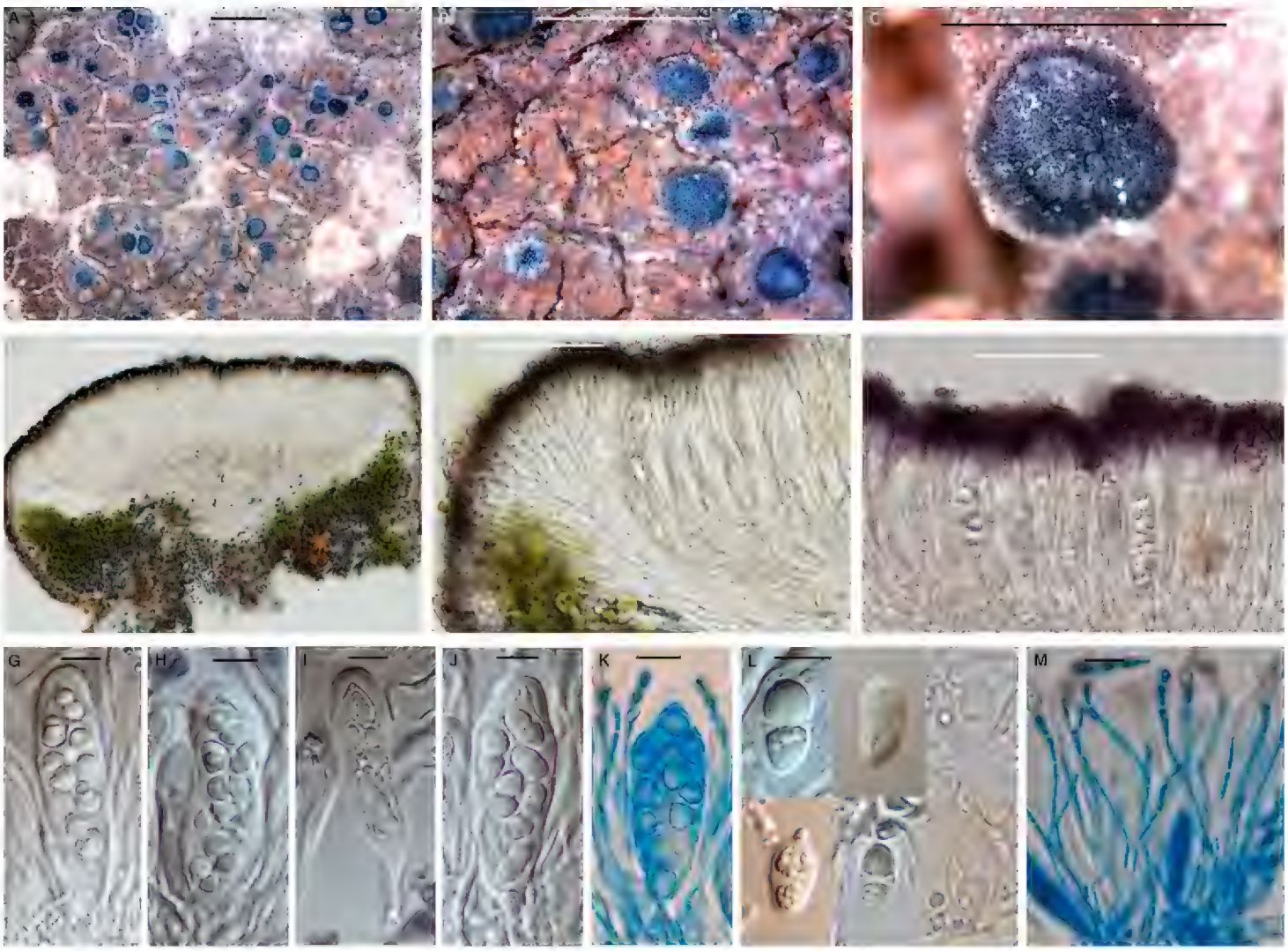

Figure 6. *Pyrenodesmia rugosa* (BDNA-L-0001102, holotype) in morphology **A–C** habitus and apothecia. Rugose thallus brown with orange spots and without pruina, but black apothecia often white pruinose **D–E** zeorine apothecia with well-developed parathecium. Algal layers continue to the base and underlying the hypothecium **F** epihymenium K+ purple and tiny granules not dissolving in K **G–K** asci oblong to narrowly clavate with eight spores **K** in the lactophenol cotton blue **L** ascospores simple in the beginning and developed polarilocular at maturity **M** paraphyses anastomosing in lactophenol cotton blue. Paraphysis tips slightly swollen. Scale bars: 1 mm (**A–C**); 100 μm (**D**); 50 μm (**E, F**); 10 μm (**G–M**).

Huriella aeruginosa **B.G. Lee & J.-S. Hur, sp. nov.**
MycoBank No: 839185
Fig. 7

Diagnosis. *Huriella aeruginosa* differs from '*Squamulea*' *chelonia* by dark greenish-grey to grey thallus without pruina (vs. yellow orange to deep orange thallus with white pruina), gold to yellow-brown epihymenium (vs. orange epihymenium), larger ascospores (7.5–12 × 4.5–7.5 μm vs. 8–10.4 × 4.7–6.0 μm) and the chemistry (thallus K–, KC– and no substance vs. thallus K+ purple, KC± purplish and the presence of parietin, teloschistin, fallacinal, parietinic acid and emodin).

Type. South Korea, Gangwon Province, Gangneung, Okgye-myeon, Mt. Seokbyung (summit), 37°35.21'N, 128°53.87'E, 1,072 m alt., on calcareous rock, 17 June 2020, B.G.Lee & H.J.Lee 2020-000872, with *Bagliettoa baldensis*, *Catillaria lenticularis*, *Endocarpon subramulosum* Y. Joshi & Hur, *Laundonia flavovirescens*, *Rusavskia elegans* and *Verrucaria nigrescens* (holotype: BDNA-L-0001072!; GenBank MW832829 for ITS).

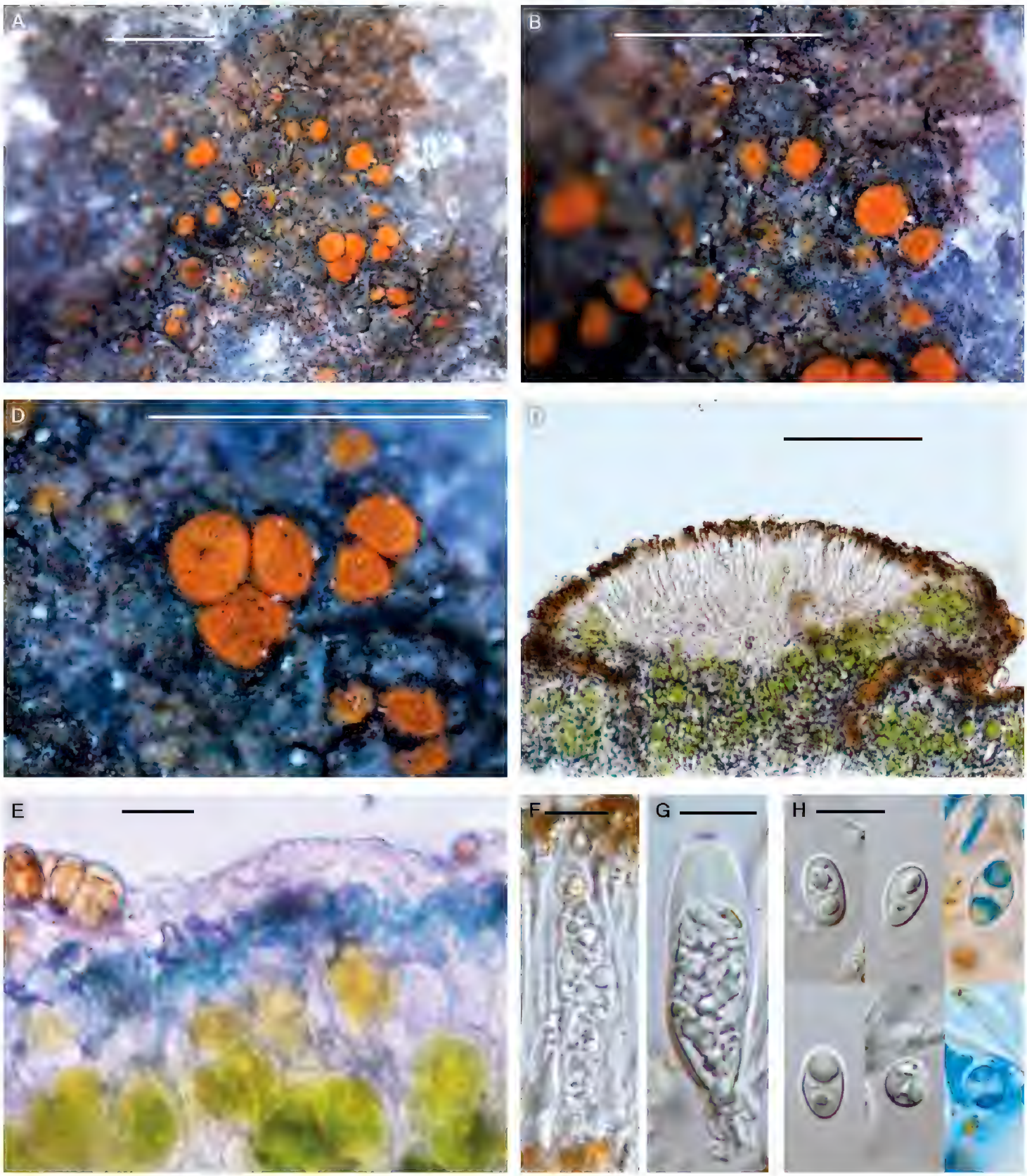

Figure 7. *Huriella aeruginosa* (BDNA-L-0001072, holotype) in morphology **A–C** habitus and apothecia. Thallus dark greenish-grey to grey with no pruina. Thalline margin of apothecia concolorous to disc **D** apothecia adnate or rarely sessile. Amphithecium well-developed, but parathecium inconspicuous. **E** thallus with dark green pigment layer under cortex **F–G** clavate asci containing 8-spores **H** ascospores generally ellipsoid, but occasionally globose, developing polarilocular in both types. Two blue coloured spores in lactophenol cotton blue. Scale bars: 1 mm (**A–C**); 100 μm (**D**);10 μm (**E–H**).

Thallus saxicolous (calcicolous), crustose, mainly areolate or slightly rimose, placodioid around edge, but without distinct lobes, thin, dark greenish-grey to grey, occasionally pale yellowish-grey when young, margin indeterminate or determinate when placodioid areoles are arranged around edge, vegetative propagules absent, areoles 0.3–0.7 mm diam., 150–200 μm thick; cortex hyaline with dark green pigment

layer, 15–25 μm thick, cortical cells granular, coarsely anticlinally arranged, 5–10 μm diam., with epinecral layer, up to 5 μm thick; medulla 80–100 μm thick, below algal layer, with large crystals (materials of substrate possibly) and brown cells (dead algal cells possibly); photobiont coccoid, cells globose to oval, 5–25 μm. Small crystals in cortex, medulla and between algal cells, dissolving in K. Prothallus absent.

Apothecia abundant, scattered and not concentrated in centre, rounded, often contiguous when mature, emerging on the surface of thallus, immersed, adnate or rarely sessile, constricted at the base, 0.2–0.4 mm diam. Disc flat when young and flat or slightly convex when mature, not pruinose, orange from the beginning, 110–230 μm thick; margin persistent, even to disc or slightly prominent, generally entire or slightly crenulate, thalline margin concolorous to disc, proper margin inconspicuous. Amphithecium well-developed, with small crystals between algal cells, dissolving in K, 50–55 μm wide laterally, algal layers continuous to the base or solitarily remaining in amphithecium, algal cells 5–25 μm diam., cortical layer hyaline with gold to yellow-brown pigment concolorous to epihymenium at periphery, 15–20 μm thick. Parathecium inconspicuous, hyaline but gold to yellow-brown at periphery, ca. 10 μm wide laterally and ca. 20 μm wide at periphery. Epihymenium gold to yellow-brown, granular, pigment K+ wine red and dissolved, 10–20 μm high. Hymenium hyaline, 45–55 μm high. Hypothecium hyaline, 35–45 μm high. Oil droplets present, small, along paraphyses and more in the base of hymenium and hypothecium. Paraphyses septate, anastomosing, 2–3 μm wide, simple or branched at tips, tips swollen or slightly swollen, not pigmented, 3.5–5.5 μm wide. Asci clavate, 8-spored, 35–48 × 14–17 μm (n = 5). Ascospores generally ellipsoid, occasionally globose, 1-septate, polarilocular or narrow septum remaining, hyaline permanently, 7.5–12 × 4.5–7.5 μm (mean = 9.9 × 5.7 μm; SD = 0.9(L), 0.6(W); L/W ratio 1.2–2.3, ratio mean = 1.8, ratio SD = 0.2; n = 104), globose spores 7.5–9 × 7.0–9.2 μm (mean = 8.0 × 7.7 μm; SD = 0.8(L), 0.9(W); L/W ratio 1.0–1.1, ratio mean = 1.0, ratio SD = 0.1; n = 11). Pycnidia not detected.

Chemistry. Thallus K–, KC–, C–, Pd–. Apothecia K+ wine red. Epihymenium K+ wine red. Epihymenium and hymenium I+ blue. UV–. No lichen substance was detected by TLC.

Distribution and ecology. The species occurs on the calcareous rock. The species is currently known from the type collection.

Etymology. The species epithet indicates the lichen's thallus colour, dark green, which is the key characteristic distinguished from all the species in the genus *Huriella*.

Notes. The morphological classification of the new species is not clear between *Huriella* and *Squamulea* because the new species has some characteristics for the former genus and others for the latter, i.e. the new species represents mainly areolate thallus without lobed margin and smaller apothecia for the former, whilst showing some squamulose thallus and wider ascospores for the latter (Table 2). The molecular results concluded the new species classification into the former genus, *Huriella*.

The new species is unique with the key characteristics of green pigmented thallus (with a distinct green layer in a section) and the substrate preference to calcareous rocks amongst all *Huriella* species.

Table 2. Comparison of the new species with two type species in *Huriella* and *Squamulea*.

Species	Huriella aeruginosa	Huriella loekoesiana	Squamulea subsoluta
Thallus	mainly areolate, rimose or placodioid around edge, but without lobes	areolate (not squamulose)	squamulose, areolate or subsquamulose, margin slightly lobed
Apothecia (mm in diam.)	0.2–0.4	0.2–0.4(–0.5)	0.1–0.6
Ascospores (μm)	7.5–12 × 4.5–7.5	(8.5–)9–11(–12) × (4.5)5–6	9.5–12.5 × 5.5–7
Molecular phylogeny	Huriella	Huriella	Squamulea
Reference	–	Kondratyuk et al. 2017b	Nash III et al. 2007; Arup et al. 2013

The new species is similar to '*Squamulea*' *chelonia*, *Squamulea galactophylla*, '*Squamulea*' *humboldtiana*, *S. parviloba* and *S. subsoluta* in the substrate preference to calcareous rocks. However, the new species is different from '*Squamulea*' *chelonia* by dark greenish-grey to grey thallus without pruina (vs. yellow orange to deep orange thallus with white pruina), gold to yellow-brown epihymenium (vs. orange epihymenium), larger ascospores (7.5–12 × 4.5–7.5 μm vs. 8–10.4 × 4.7–6.0 μm) and the chemistry (thallus K–, KC– and no substance vs. thallus K+ purple, KC± purplish and the presence of parietin, teloschistin, fallacinal, parietinic acid and emodin) (Bungartz et al. 2020).

The new species differs from *S. galactophylla* by thallus colour (dark greenish-grey to grey vs. dirty white to yellowish-brown), flat to convex disc (vs. flat disc only), yellowish-orange apothecia (vs. cinnamon-brown apothecia), smaller ascospores (7.5–12 × 4.5–7.5 μm vs. 10–15 × 5–7 μm) (Fink 1935; Arup 2013).

The new species is distinguished from '*Squamulea*' *humboldtiana* by dark greenish-grey to grey thallus without pruina (vs. yellow-orange to deep orange thallus with pruina), absence of prothallus (vs. presence of prothallus), larger ascospores (7.5–12 × 4.5–7.5 μm vs. 8.1–9.9 × 4.8–5.9 μm) and the chemistry (thallus K–, KC– and no substance vs. thallus K+ purple, KC± purplish and the presence of parietin, teloschistin, fallacinal, parietinic acid and emodin) (Bungartz et al. 2020).

The new species differs from *S. parviloba* by dark greenish-grey to grey thallus (vs. yellow-orange to orange thallus), absence of lobes (vs. short narrow elongated lobes around edge), convex and yellow-orange disc (vs. flat and deep orange disc), smaller ascospores (7.5–12 × 4.5–7.5 μm vs. 11–14 × 5.5–7 μm) and the chemistry (thallus K– vs. thallus K+ red) (Wetmore 2003; Nash III et al. 2007).

The new species is different from *S. subsoluta by* dark greenish-grey to grey thallus (vs. yellow-orange, orange to reddish-orange thallus), absence of prothallus (vs. black prothallus), flat to convex, yellow-orange apothecia (vs. flat to concave, deep orange apothecia) and the chemistry (thallus K– and no substance vs. thallus K+ red, the presence of parietin, fallacinal, emodin and teloschistin) (Wetmore 2003; Nash III et al. 2007).

The most distinctive characteristic of the new species is the thallus colour, i.e. dark greenish-grey to grey, which is different from all comparable calcicolous species in the genus *Squamulea*.

Key to the species of *Huriella* and *Squamulea* (20 taxa)

Although some species of *Huriella* have distinct characteristics, different from *Squamulea*, such as mainly areolate and non-squamulose thallus without lobes at margin, smaller apothecia and narrower ascospores (Kondratyuk et al. 2017b), those morphological taxonomic keys do not clearly separate the two genera concerning all known species in the genera. The morphological characteristics are assumingly based on the comparison between type species of the comparable genera, but several species do not correspond to the characteristics (e.g. *Huriella aeruginosa*, *H. flakusii* Wilk and *H. salyangiana* S.Y. Kondr. & Hur with squamulose thalli), although those species are classified in the genus *Huriella* in molecular phylogeny. Such a discrepancy between morphology and molecular phylogeny occur in *Squamulea squamos*a (B. de Lesd.) Arup, Søchting & Frödén and *S. subsoluta* as well. Both species are considered conspecific in morphology. Both species are very similar in morphology and ecology occurring together on the same rock. Whereas the only difference between them is that the former has a thalline margin and it is lacking in the latter (Nash III et al. 2007), the latter representing a permanent thalline margin from the Galapagos Islands as well (Bungartz et al. 2020). However, the two species are separated and located distant from each other in molecular results of this study (Fig. 5). Nevertheless, those are still considered conspecific in the key below as a taxonomic key is based mainly on ecology, morphology and chemistry. The genera *Huriella* and *Squamulea* should be more studied in the future and here a preliminary key is updated from previous taxonomic keys of Wetmore (2003) and Bungartz et al. (2020).

1 Not directly on rock, but on lichen or bone **2**
– On rock **4**
2 On lichen (*Aspicilia*) living on rock ..... ***Squamulea nesodes***
– On bone **3**
3 Thallus generally areolate, without blastidia, not pruinose ..... ***'Squamulea' osseophila***
– Thallus generally (sub)squamulose, blastidia abundant, not pruinose or faintly orange pruinose on thallus ..... ***'Squamulea' phyllidizans***
4 On calcareous rocks **5**
– On siliceous rocks **10**
5 Thallus pruinose **6**
– Thallus not pruinose **7**
6 Thallus angular, areolate to subsquamulose, prothallus absent ..... ***'Squamulea' chelonia***
– Thallus areolate or bullate, prothallus black when present ..... ***'Squamulea' humboldtiana***
7 Thallus whitish, greyish or greenish **8**
– Thallus yellow-orange to orange **9**
8 Thallus dirty whitish, disc cinnamon-brown ..... ***Squamulea galactophylla***
– Thallus dark greenish-grey to grey, disc orange ..... ***Huriella aeruginosa***

9 Areole margins with small lobules ..... ***Squamulea parviloba***
– Areole margins without lobules ..... ***Squamulea squamosa* (*S. subsoluta*)**
10 With blastidia or soredia **11**
– Without blastidia or soredia **13**
11 Thallus brownish-orange, apothecia rare, disc reddish to reddish-brown, ascospores 11–16 × 6–8 µm, isthmus 1–3 µm ..... ***Squamulea kiamae***
– Thallus yellowish-orange to deep orange, apothecia common, disc concolorous to thallus or slightly deeper, ascospores 8.4–13.3 × 5–7.1 µm, isthmus 2.5–4.6 µm **12**
12 Blastidia abundant, sometimes faintly orange pruinose on thallus, but not pruinose on disc ..... ***'Squamulea' phyllidizans***
– Soredia rarely present, rarely white pruinose on disc, but not pruinose on thallus ..... ***Squamulea squamosa* (*S. subsoluta*)**
13 Thallus areolate to (sub)squamulose **14**
– Thallus areolate or bullate, but not squamulose **21**
14 Prothallus distinctly blackened ..... ***'Squamulea' oceanica***
– Prothallus absent **15**
15 Disc brownish to reddish or blackish **16**
– Disc orangish **19**
16 Thallus orange, disc reddish, ascospores 11–14.2 × 5.9–7.5 µm ..... ***Huriella flakusii***
– Thallus brownish, disc pale brown, brownish-orange to blackish-brown **17**
17 Disc dark brown-orange to black-brown, hypothecium 20–30 µm high, ascospores 7–9 × 4.5–6.5 µm ..... ***Huriella salyangiana***
– Disc pale brown to brownish-orange, hypothecium 50–150 **µm** high, ascospores 9–13 × 4.5–6 µm **18**
18 Disc 0.4–0.9 mm diam., hypothecium 50–100 µm high, ascospores 9–13 × 5–6 µm ..... ***Squamulea coreana***
– Disc 0.2–0.4 mm diam., hypothecium 100–150 µm high, ascospores 10–10.5 × 4.5–6 µm ..... ***Squamulea uttarkashiana***
19 Areole margins with small lobules ..... ***Squamulea parviloba***
– Areole margins without lobules **20**
20 Ascospores 8–10.4 × 4.7–6 µm, isthmus 2.1–3.3, not pruinose on disc ..... ***'Squamulea' chelonia***
– Ascospores 8.4–13.3 × 5.2–7 µm, isthmus 2.5–4 µm, rarely pruinose on disc ..... ***Squamulea squamosa* (*S. subsoluta*)**
21 Thallus yellow-orange to deep orange, prothallus black when present, ascospores 8.1–9.9 × 4.8–5.9 µm, isthmus 2.7–3.2 µm ..... ***'Squamulea' humboldtiana***
– Thallus yellow-brownish or yellow-greenish, prothallus absent, ascospores 9–15 × 5–8 µm, isthmus 2–5 µm **22**
22 Apothecia 0.2–0.3 mm diam., disc dull brown, dull yellow to bright yellow... ..... **23**
– Apothecia 0.3–1 mm diam., disc orange, brownish-yellow to reddish-orange **24**

23 Disc dull yellow to bright yellow, hymenium 50–60 µm high, hypothecium 20–30 µm high, ascospores 9–11 × 5–6 µm, isthmus 4–5 µm ..... ***Huriella loekoesiana***

– Disc dull brown, hymenium 80–100 µm high, hypothecium 80–110 µm high, ascospores 13–14.5 × 7–8 µm, isthmus 3–4 µm.... ***Huriella upretiana***

24 On mountain, thallus yellow-brown, disc orange, isthmus 3–4 µm..... ***Squmulea micromera***

– On coast, thallus dull green-yellow to yellow-brown, disc orange to red-orange, isthmus 2–3 µm.....***Huriella pohangensis***

Acknowledgements

This work was supported by a grant from the Korean National Research Resource Center Program (NRF-2017M3A9B8069471).

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